

# Phylogenetic position of the bivalve family Cyrenoididae—removal from (and further dismantling of) the superfamily Lucinoidea

John D. Taylor

Emily A. Glover

Suzanne T. Williams

Department of Zoology  
The Natural History Museum  
London, SW7 5BD UNITED KINGDOM  
j.taylor@nhm.ac.uk  
emilyglover@mac.com  
s.williams@nhm.ac.uk

---

## ABSTRACT

A molecular analysis using sequences from 18S and 28S rRNA genes of the brackish and freshwater bivalve *Cyrenoida floridana*, in conjunction with a wide range of other heterodont bivalves, demonstrated a close relationship with the families Corbiculidae and Glauconomidae and distant from the Lucinoidea, where the Cyrenoididae had been usually classified. Based on this result it is proposed that the Cyrenoididae be removed from the Lucinoidea, which, for living taxa, now includes only the family Lucinidae.

*Additional Keywords:* Bivalvia, Heterodonta, *Cyrenoida floridana*, 18S rRNA, 28S rRNA

---

## INTRODUCTION

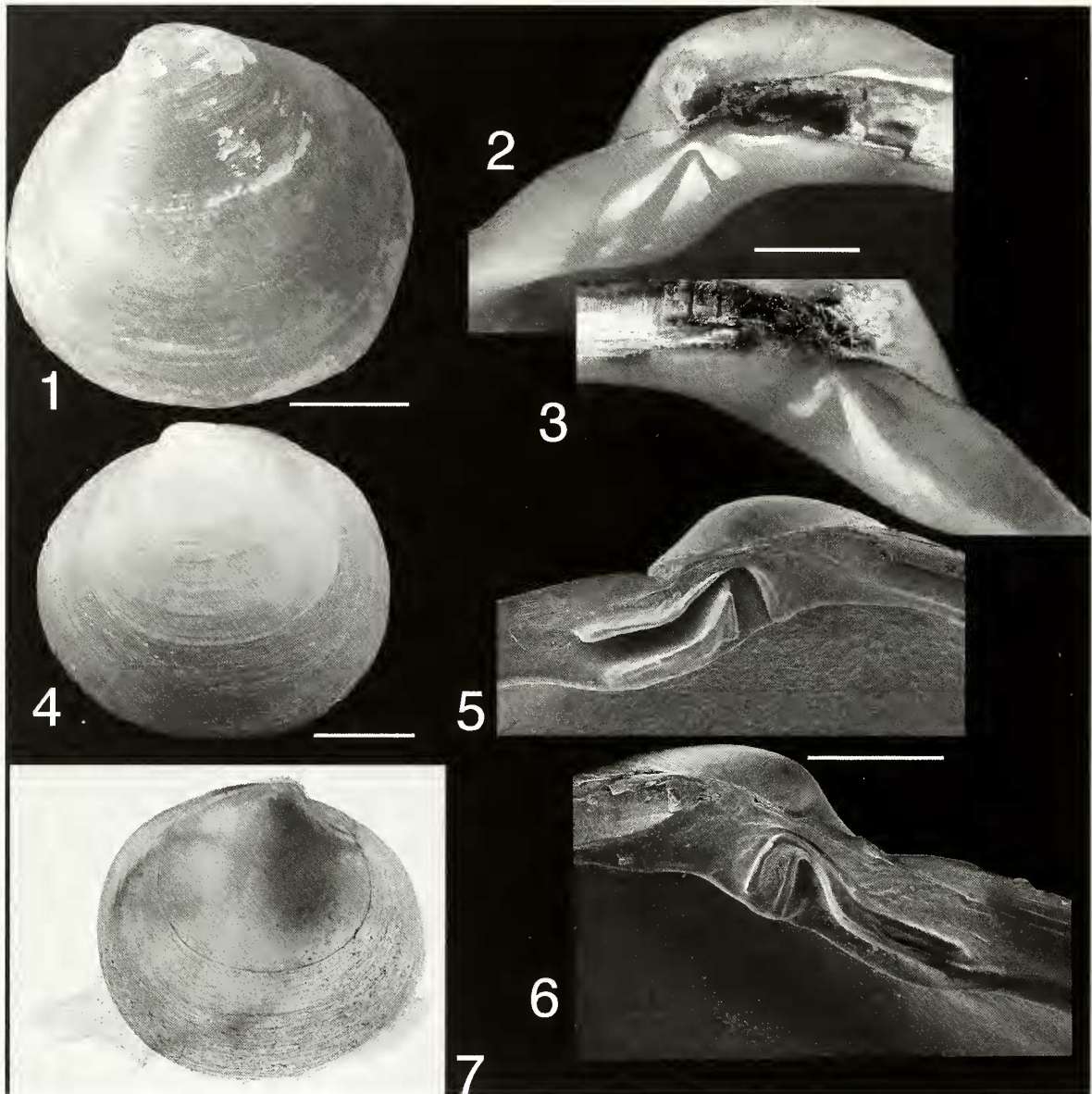
Until recently, most classifications of bivalve mollusks included within the superfamily Lucinoidea several component families (Lucinidae, Fimbriidae, Thyasiridae, Ungulinidae, Cyrenoididae, and fossil Mactromyidae) (e.g. Dall, 1901; Chavan, 1969; Boss, 1982; Vaught, 1989; Amler, 1999). The Lucinidae and some Thyasiridae are notable for the chemosymbiosis with sulphide-oxidizing bacteria housed in the ctenidia (Southward, 1986; Taylor and Glover, 2006). Molecular analyses of the Lucinoidea, compared with a wide range of other heterodont bivalves, demonstrated that superfamily was not monophyletic, with the Thyasiridae and Ungulinidae not closely related to the Lucinidae (Williams, Taylor, and Glover, 2004; Taylor, Williams, and Glover, 2007; Taylor et al., 2007). The Ungulinidae group near families such as the Veneridae, Corbiculidae, and Mactridae, while the Thyasiridae form a basal clade within the Euheterodonta and are considered as a distinct superfamily—Thyasiroidea. *Fimbria fimbriata*, one of the two living species of Fimbriidae, nested together

with Lucinidae species, with no support for separate familial status, and the nominal family was synonymized accordingly. Apart from the Lucinidae, the only other family with living species still classified within Lucinoidea is the Cyrenoididae, but lack of suitably preserved material has precluded inclusion in molecular analyses. From morphological evidence, Williams et al. (2004) and Taylor and Glover (2006) thought a relationship to the Lucinidae unlikely, *Cyrenoida* having medium to long fused siphons, well developed labial palps and ctenidia with two demibranchs. These statements led Bieler and Mikkelsen (2006) to place Cyrenoididae as *incertae sedis*.

The Cyrenoididae Adams and Adams, 1857 (= Cyrenellidae Gray, 1853) comprise a small group of around ten nominal species of little-studied bivalves inhabiting brackish to freshwaters, classified into a single genus, *Cyrenoida* (type species *C. dupontia* Joannis, 1835) (Figures 1–3), distributed in western Africa, eastern and western Americas and some islands of the Caribbean. The West African species inhabit brackish mangrove habitats (Pilsbry and Bequaert, 1927). In the eastern USA, *Cyrenoida floridana* Dall, 1901 (Figures 4–7) ranges from Delaware to the coast of the Gulf of Mexico, maybe as far west as Yucatan (Vokes and Vokes, 1983), where it inhabits fresh and brackish water habitats (Leathem, Kinner, and Maurer, 1976; Kat, 1982; Bishop and Haekney, 1987).

Dall (1895) was the first to place the Cyrenoididae within the Lucinoidea, stating (p. 545) “These are estuarine Lucinea.” Later (Dall, 1901: 817) stated “. . . shells of this group with a Lucinoid animal and *Diplodontia*-like shell, exhibit a hinge structure which is wholly distinct from any other of the Lucinea.” Many later classifications, including the influential Treatise of Invertebrate Paleontology (Chavan, 1969), followed Dall in placing the Cyrenoididae within the Lucinoidea (e.g. Vokes, 1980; Boss, 1982; Vaught, 1989; Skelton and Benton, 1993; Amler, 1999).

---



**Figures 1-7.** *Cyrenoida dupontia* (1-3) and *C. floridana* (4-7). **1.** *Cyrenoida dupontia* Joannis, left valve, Senegal (BMNH 20081055). Scale bar = 10 mm. **2-3.** Hinge teeth of *Cyrenoida dupontia*, right valve (2) and left valve (3). Scale bar = 2 mm. **4.** *Cyrenoida floridana* Dall, left valve, Blue Hole, Big Pine Key, Florida (BMNH 20081054). Scale bar = 2 mm. **5-6.** Hinge teeth (SEM images) of *Cyrenoida floridana*, right valve (5) and left valve (6) (BMNH 20081054). Scale bar = 500  $\mu$ m. **7.** *Cyrenoida floridana*, living specimen with short, fused siphons, Blue Hole, Big Pine Key, Florida. (Photo R. Bieler, September 2007).

Nevertheless, different opinions were expressed by other authors, Fiseher (1887: 1096), for example, placed Cyrenoididae (as Cyrenellidae) into a suborder Conehaea, near to *Corbicula* and Ungulinidae but apart from the Lucinoidea. While Thiele (1934) included Cyrenoididae with other fresh and brackish water bivalves in the *stirps* Sphaeriacea but not positioned closely to Lucinoidea. The family was elevated to superfamily status by Olsson (1961: 227) but placed near to Lucinoidea, a decision also followed by Keen (1971). The superfamily Cyrenoidoidea was also recognized by Neveeskaya et al. (1971) and

placed along with Lueinoidea in the order Astartida. Alternatively, and rather bizarrely, Starobogatov (1992) placed Cyrenoidoidea within the infraorder Eryeinoinei along with Cyamioidea, Galeommatoidea and Leptonoidea, all contained within the order Luciniformes.

Clearly, there exists much uncertainty concerning the phylogenetic position of Cyrenoididae amongst the heterodont bivalves but this has never been tested by either morphological or molecular analyses. In 2007, we obtained samples of *Cyrenoida floridana* suitable for molecular analysis and in this paper we present 18S and



28S rRNA sequences for the species that enable us to establish the phylogenetic position of the family in relation to a wide range of heterodont bivalve taxa previously analysed (Taylor et al., 2007) and specifically address the question of whether the Lucinidae and Cyrenoididae form a monophyletic group.

## MATERIALS AND METHODS

The sample of *Cyrenoida floridana*, preserved in 100% ethanol (BMNH 20081053), was collected (18 September 2007) from Blue Hole (24°42.4' N, 81°22.8' W) a freshwater pond on Big Pine Key, Monroe County, Florida Keys, Florida, USA, from shoreline mud up to 0.5 m depth among roots of marginal reeds. Other material from the same site is lodged at the Field Museum of Natural History (FMNH 314434; 317667).

For the molecular analysis, methods of DNA extraction, amplification and sequencing followed by sequence analysis and phylogenetic reconstruction are as described in Taylor et al. (2007). Sequences for *Cyrenoida floridana* were analysed together with the data set of heterodonts listed in Taylor et al. (2007, Table 1), with the addition of new 18S and 28S sequences for *Mya arenaria* Linnaeus, 1758 (family Myidae) from Gdynia, Poland. The new sequences for *Cyrenoida floridana* and *Mya arenaria* are lodged in GenBank (Accession numbers: *C. floridana* FM999789, FM999790; *M. arenaria* FM999791, 779792). Voucher specimens of both species are housed in the Department of Zoology, The Natural History Museum, London.

Phylogenies were constructed using Bayesian methods (MrBayes v3.1.2, Huelsenbeck and Ronquist, 2001) using a GTR+G+I model. The analysis for each data set was run for 3,500,000 generations, with a sample frequency of 100. Each analysis was run twice. The first 15,000 trees from each run were discarded so that the final consensus tree was based on the combination of accepted trees from each run (a total of 40,000 trees). Support for nodes was determined using posterior probabilities (PP, calculated by MrBayes).

## RESULTS

The combined tree based on concatenated sequences from 18S rRNA and 28S rRNA genes is shown in Figure 8. The individual trees based on single genes are very similar in topology to those published previously (Taylor et al., 2007). In all analyses *Cyrenoida floridana* nests in a highly supported clade with *Corbicula fluminea* (Corbiculidae) and *Glaucanome virens* (Glauconomidae). This clade forms part of a major group of heterodonts named Neoheterodontei by Taylor et al. (2007). *Cyrenoida* is widely separated from both Thyasiridae and Lucinidae that appear in the more basal parts of the tree. The Ungulinidae, although also a member of the Neoheterodontei, form a separate clade distinct from *Cyrenoida*.

## DISCUSSION

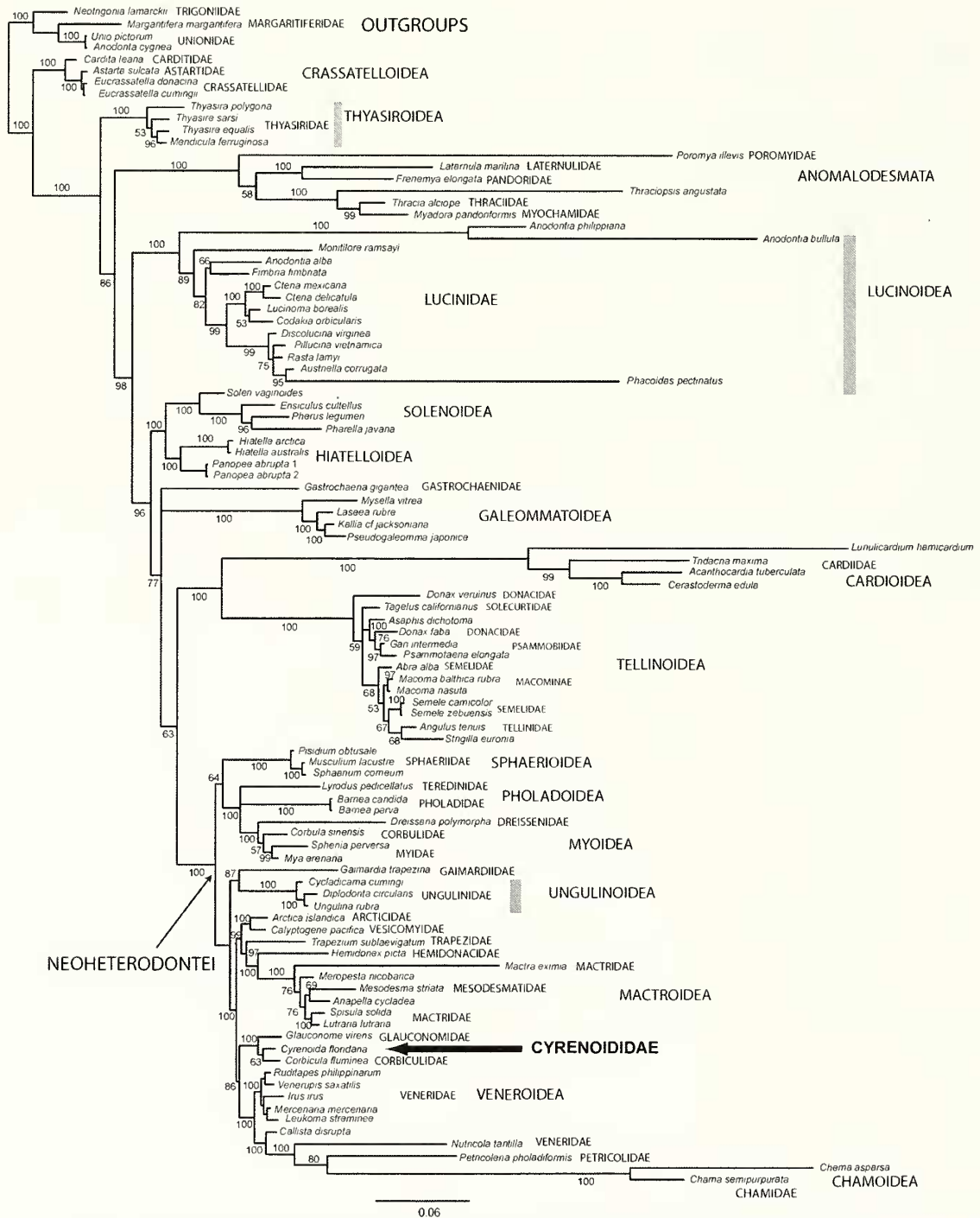
It would have been desirable to have included the type species of *Cyrenoida*, namely, *Cyrenoida dupontia* Joannis, 1835, from West Africa, in the molecular analysis but no suitably preserved material was available. Although a much smaller species, *C. floridana* is similar to *C. dupontia* in shell characters, notably the unusual hinge dentition, and we feel confident that they are members of the same group. *Cyrenoida dupontia* has three cardinal teeth in the right valve, the anterior of these is thin and elongate and the central tooth larger and slightly bifid (Figures 2–3) while the left valve has two cardinals, the posterior tooth smaller and bifid and the anterior tooth elongate. Lateral teeth are absent. The dentition of *C. floridana* is very similar (Figures 4–6) with three cardinal teeth in the right valve, the central being larger and two cardinal teeth in the left valve with the posterior tooth bifid and the anterior tooth elongate. We have also examined the gross anatomy of *Cyrenoida rosea* (d'Ailly, 1896) from Nigeria (National Museum of Wales specimen NMW.Z.2003.029.02041) and this has ctenidia with two demibranchs, with the inner demibranch larger, paired triangular labial palps, and fused medium-length posterior siphons. *Cyrenoida floridana* is similar, with small outer demibranchs, triangular labial palps and short fused posterior siphons, the inhalant with papillae (Figure 7). Despite the presence of siphons, there is no pallial sinus in any *Cyrenoida* species.

The main conclusion of this study, based on our results for *Cyrenoida floridana*, is that the Cyrenoididae should be removed from the Lucinoidea and classified close to, or possibly within, the Corbiculoidea. The status of *Cyrenoida* in relation to Corbiculidae and Glauconomidae needs further analysis with a larger dataset of corbiculid species. For the present the family can be classified within a separate superfamily Cyrenoidoidea as proposed by Olsson (1961). Molecular evidence for a highly supported relationship between Corbiculidae and Glauconomidae was reported by Taylor et al. (2007) although the elongate shells with deep pallial sinus and long siphons of *Glaucanome* are less similar morphologically to Cyrenoididae and Corbiculidae. Species of Cyrenoididae and Corbiculidae occur in both brackish and freshwater habitats while Glauconomidae live intertidally among mangroves in environments of fluctuating salinity.

For living taxa, we consider that the superfamily Lucinoidea should now include only the family Lucinidae, with the families Thyasiridae, Ungulinidae and Cyrenoididae excluded. The position of the entirely fossil families Mactromyidae, Ilionidae, and Paracyclidae is unresolved although the latter two embrace species with lucinid characters.

## ACKNOWLEDGMENTS

It is a pleasure to thank Rüdiger Bieler and Petra Sierwald for generous hospitality and help in collection of



**Figure 8.** Molecular phylogeny of heterodont bivalves including *Cyrenoida* produced by Bayesian analysis for concatenated sequences from 18S and 28S rRNA genes. The tree was drawn using members of the palaeoheterodonte Trigoniidae, Unionidae, and Margaritiferidae as outgroups. Support values are posterior probabilities. Nodes with <50% support have been collapsed. Positions of Lucinoidea, Thysiroidea, and Ungulinoidea marked by grey bars. Details of taxa in Taylor et al. (2007).

*C. floridana*. We are grateful to Pat Dyal for assistance with molecular analysis and to Graham Oliver (National Museum of Wales) for making a specimen of *Cyrenoida rosea* available. We thank Professor Phil Rainbow and Department of Zoology, NHM for continuing support.

Research on this exemplar species in the Bivalve Tree-of-Life project ([www.bivatol.org](http://www.bivatol.org) <<http://www.bivatol.org/>>) was supported by the U.S. National Science Foundation AToL program (DEB-0732854/0732903/0732860). The specimens were collected under U.S. Fish and Wildlife

Service Special Use Permit 41580-2007-11 (to Rüdiger Bieler) for research on native molluscan species in the National Key Deer Refuge.

#### LITERATURE CITED

- Adams, H. and A. Adams. 1853–58. The genera of recent Mollusca, arranged according to their organization. van Hoorst. London, 3 volumes. Volume 2. Cyrenoididae, p. 452 (published 1857).
- d'Ailly, A. 1896. Contributions à la connaissance des mollusques terrestres et d'eau douce de Kaméroun. Bihang Till Kongliga Svenska Vetenskaps-Akademiens Handlingar 22: 1–137.
- Amler, M.R.W. 1999. Synoptical classification of fossil and Recent Bivalvia. *Geologica et Palaeontologica* 33: 237–248.
- Bieler, R. and P.M. Mikkelsen. 2006. Bivalvia—a look at the branches. *Zoological Journal of the Linnean Society* 148: 223–235.
- Bishop, T.D. and C.T. Hackney. 1987. A comparative study of the mollusc communities of two oligohaline intertidal marshes: spatial and temporal distribution of abundance and biomass. *Estuaries* 10: 141–152.
- Boss, K.J. 1982. Mollusca. In: Parker, S.P. (Ed.). *Synopsis and classification of living organisms*. McGraw-Hill, New York, pp. 945–1166.
- Dall, W.H. 1895. Contribution to the Tertiary fauna of Florida, with especial reference to the Miocene silex-beds of Tampa and the Pliocene beds of the Caloosahatchee River. Part III. A new classification of the Pelecypoda. *Wagner Free Institute of Science of Philadelphia Transactions* 3(3): 479–570.
- Dall, W.H. 1901. Synopsis of the Lucinacea and of the American species. *Proceedings of the U.S. National Museum* 23: 779–833.
- Chavan, A. 1969. Superfamily Lucinacea Fleming, 1828. pp. N491–N518. IN Moore, R. C. [ed.]. *Treatise on Invertebrate Paleontology, Part N, Mollusca 6, Bivalvia, (2)*. Geological Society of America, Boulder, and University of Kansas Press, Lawrence, 951 pp.
- Fischer, P.H. 1880–87. *Manuel de conchyliologie et de paléontologie conchyliologique*. F. Savy, Paris. 1369 pp.
- Gray, J.E. 1853. A revision of the genera of some of the families of Conchifera or Bivalve shells. *Annals and Magazine of Natural History, series 2*, 11: 33–44.
- Huelsenbeck, J.P. and Ronquist, F. 2001. MRBAYES: Bayesian inference of phylogenetic trees. *Bioinformatics* 17: 754–755.
- Joannis, L. de. 1835. Observations sur plusieurs Mollusques dont on ne connaissait que les coquilles, et descriptions des ces mollusques, et de quelques espèces inédites ou non figurées jusqu'à ce jour. *Magasin de Zoologie* 5: pls. 36–64.
- Kat, P.W. 1982. Reproduction in a peripheral population of *Cyrenoida floridana* (Bivalvia: Cyrenoididae). *Malacologia* 23: 47–54.
- Keen, A.M. 1971. *Sea Shells of Tropical West America: Marine Mollusks from Baja California to Peru*. 2<sup>nd</sup> edition. Stanford University Press, Stanford, 1064 pp.
- Leathaem, W., P. Kinner, and D. Maurer. 1976. Northern range extension of the Florida marsh clam *Cyrenoida floridana* (Superfamily Cyrenoidacea). *The Nautilus* 90: 93–94.
- Neveeskaya, L.A., O.A. Scarlato, Y.I. Starobogatov, and A.G. Eberzon. 1971. New ideas on bivalve systematics. *Paleontological Journal*, 1971 (2), 141–155. Translation from *Russian of Paleontologicheskii Zhurnal* 1971 (2): 3–20.
- Olsson, A.A. 1961. Mollusks of the tropical eastern Pacific particularly from the southern half of the Panamic-Pacific faunal province (Panama to Peru). *Panamic Pacific Pelecypoda*. Paleontological Research Institution, Ithaca, 574 pp.
- Pilsbry, H.A. and J. Bequaert. 1927. The aquatic mollusks of the Belgian Congo with a geographical and ecological account of Congo malacology. *Bulletin of the American Museum of Natural History* 53: 69–659.
- Skelton, P.W. and M.J. Benton, 1993. Mollusca: Rostroconchia, Scaphopoda and Bivalvia. In: Benton, M.J. (ed.) *The Fossil Record 2*. Chapman & Hall, London, pp. 237–263.
- Southward, E.C. 1986. Gill symbionts in thyasirids and other bivalve molluscs. *Journal of the Marine Biological Association of the United Kingdom* 66: 889–914.
- Starobogatov, Y.I. 1992. Morphological basis for phylogeny and classification of Bivalvia. *Ruthenica* 2: 1–25.
- Taylor, J.D. and E.A. Glover. 2006. Lucinidae (Bivalvia)—the most diverse group of chemosymbiotic molluscs. *Zoological Journal of the Linnean Society* 148: 421–438.
- Taylor, J.D., S.T. Williams, and E.A. Glover. 2007. Evolutionary relationships of the bivalve family Thyasiridae (Mollusca: Bivalvia), monophyly and superfamily status. *Journal of the Marine Biological Association of the United Kingdom* 87: 565–574.
- Taylor, J.D., S.T. Williams, E.A. Glover, and P. Dyal. 2007. A molecular phylogeny of heterodont bivalves (Mollusca: Bivalvia: Heterodonta): new analyses of 18S rRNA and 28S rRNA genes. *Zoologica Scripta* 36: 587–606.
- Thiele, J. 1934. *Handbuch der systematischen Weichtierkunde* 2 (3) (Scaphopoda. Bivalvia. Cephalopoda). Fischer, Jena, pp. 779–1022.
- Vaught, K.C. 1989. *A classification of the living Mollusca*. American Malacologists, Melbourne, Florida, 196 pp.
- Vokes, H.E. 1980. *Catalogue of the Bivalvia: a systematic and bibliographic catalogue (revised and updated)*. Paleontological Research Institution, Ithaca, 307 pp.
- Vokes, H.E. and E.H. Vokes, 1983. *Distribution of shallow-water marine Mollusca, Yucatan Peninsula, Mexico*. Tulane University Mesoamerican Ecological Institute, Monograph 1: 1–183.
- Williams, S.T., J.D. Taylor, and E.A. Glover. 2004. Molecular phylogeny of the Lucinoidea (Bivalvia): non-monophyly and separate acquisition of bacterial chemosymbiosis. *Journal of Molluscan Studies* 70: 187–202.